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On the presence of *Chthonius* (*C.*) *halberti* Kew and *Chthonius* (*C.*) *ressli* Beier in France with remarks on the status of *Kewochthonius* Chamberlin and *Neochthonius* Chamberlin (Arachnida, Chelonethida, Chthoniidae) [1]

by Mark L. I. JUDSON

Abstract. — BEIER's (1963) record of *Chthonius* (*C.*) *halberti* Kew from Banyuls-sur-Mer, France, is confirmed. *Chthonius* (*C.*) *ressli* Beier is recorded from France (La Rochelle : Charente-Maritime) for the first time and is synonymized with *C.* (*C.*) *parvulus* Inzaghi from Italy. The validity of *Kewochthonius* Chamberlin and *Neochthonius* Chamberlin is discussed. *Kewochthonius* is synonymized with *Chthonius* (*Chthonius*) C. L. Koch; *Neochthonius* is retained as a valid genus, restricted to North America. An analysis of the position of trichobothrium *est* in *Chthonius* suggests that interspecific differences in trichobothrial positions might be explained by an allometric model of chelal growth.

Résumé. — La présence de *Chthonius* (*C.*) *halberti* Kew en France (Banyuls-sur-Mer) est confirmée. *Chthonius* (*C.*) *ressli* Beier est signalée en France pour la première fois. L'espèce *Chthonius* (*C.*) *parvulus* Inzaghi d'Italie est considérée comme synonyme de *C.* (*C.*) *ressli*. La validité de *Kewochthonius* Chamberlin et de *Neochthonius* Chamberlin est discutée. *Kewochthonius* est relégué en synonymie de *Chthonius* (*Chthonius*) C. L. Koch; *Neochthonius* est maintenu au rang de genre, limité à l'Amérique du Nord. L'analyse de l'emplacement de la trichobothrie *est* dans *Chthonius* suggère qu'un modèle allométrique de croissance de la pince peut être employé pour expliquer les différences interspécifiques des positions trichobothriales.

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The genera *Kewochthonius* and *Neochthonius* were created by CHAMBERLIN (1929) for *Chthonius halberti* Kew (from England and Ireland) and *N. stanfordianus* Chamberlin (from California) respectively. At the time he noted that they migh prove to be synonymous. Since then, these two genera have been a source of confusion and nomenclatural instability.

BEIER (1931) synonymized the two genera, giving *Neochthonius* priority and reducing it to a subgenus of *Chthonius* C. L. Koch. HOFF (1951) accepted this synonymy, but gave *Kewochthonius* priority — following CHAMBERLIN's (1929) expressed intention — and returned it to generic status. The type species of *Kewochthonius* and *Neochthonius* were subsequently

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revised by MUCHMORE (1968, 1969) who concluded that both genera were valid. MAHNERT (1974) returned *Kewochthonius* to subgeneric status under *Chthonius* and suggested that all of the European species which had been assigned to *Neochthonius* should be transferred to *Kewochthonius*. However, GARDINI (1977) followed BEIER in regarding *Neochthonius* as a subgenus of *Chthonius* with priority over *Kewochthonius*. The situation has been further confused by LECLERC's (1983) proposal to limit *Kewochthonius* to the type species and transfer all of the remaining species to *Neochthonius*.

During work on material of *Chthonius* (*K.*) *halberti* and *Chthonius* (*C.*) *ressli* Beier from France it became clear that *Chthonius* and *Kewochthonius* were more closely related than one would suppose from the litterature. In order to reassess the relationships of these taxa, specimens of *Neochthonius stanfordianus* (U.S.A., California, Riverside County, Cajalco, K. W. COOPER leg., 18 February 1968; WM 1567) have also been studied.

STATUS OF *Neochthonius*

MUCHMORE (1963) separated *Neochthonius* from *Kewochthonius* on the basis of the arrangement of the coxal spines. In *Kewochthonius*, the spines are arranged in "bristle-like patches", whereas in *Neochthonius* they form a "row of nearly equally-pinnate blades". He also noted that the spines of *Neochthonius* are relatively large and have longer pinnules than those of *Kewochthonius*.

The coxal spines of *Kewochthonius* are similar in form and arrangement to those of *Chthonius*. Examination of the spines of *Chthonius* (*C.*) *ischnocheles* and *N. stanfordianus* by scanning electron microscopy confirms the differences between the two types of spines (figs. 1 and 2).

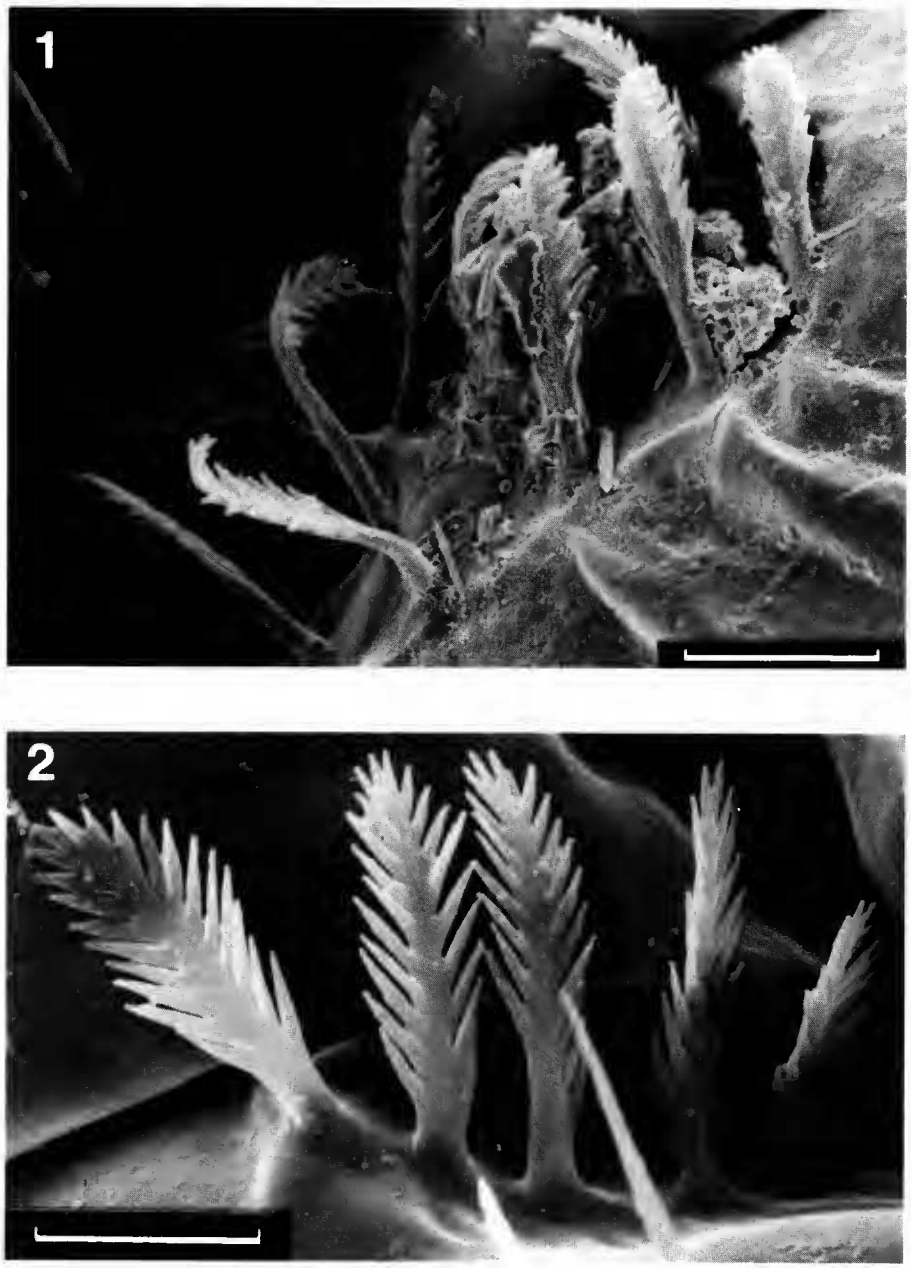
Neochthonius also appears to differ from *Chthonius* (*s.st.*) and *Kewochthonius* in the form of the female genitalia. In *Chthonius* and *Kewochthonius* the lateral apodeme frame is complete (LEGG, 1975; pers. obs.); in *Neochthonius* the frame is incomplete (fig. 10), resembling that of *Chthonius* (*Ephippiochthonius*) species.

I therefore follow MUCHMORE's (1969) interpretation of *Neochthonius* which includes three species — *N. stanfordianus* Chamberlin, *N. troglodytes* Muchmore and *N. amplus* (Schuster) — all from California.

STATUS OF *Kewochthonius*

Kewochthonius is separated from *Chthonius* by the form of the teeth of the chela : in *Kewochthonius* the teeth are rounded and contiguous, whereas in *Chthonius* they are triangular and spaced, at least for part of their length. However, several *Chthonius* species have been described with an intermediate dentition, both types of teeth being present (e.g. *C.* (*C.*) *ressli*, fig. 9). This has led to a rather arbitrary division of the two groups, reflected by the problematic positions of *Chthonius pygmaeus* Beier and *C. strinatii* Mahnert (MAHNERT, 1975, 1979).

LECLERC (1983) introduced a second character — the position of trichobothrium *est* on the fixed finger — to distinguish *Kewochthonius*/*Neochthonius* from *Chthonius*. In *Neochthonius* and *Kewochthonius*, *est* is situated more proximally than in *Chthonius*. LECLERC quantified this



FIGS. 1-2. — 1, *Chthonius* (*C.*) *ischnocheles* (Hermann), coxal spines of right coxa II; 2, *Neochthonius stanfordianus* Chamberlin, coxal spines of left coxa II. (Scale lines equal 0.01 mm.)

difference by the use of a ratio, *a*, defined as the distance from *est* to the tip of the fixed finger divided by the distance from *est* to *ist*. His analysis of a large number of species of *Kewochthonius, Neochthonius* and *Chthonius* suggested that in *Chthonius, a* is less than 0.79, whereas in *Kewochthonius/Neochthonius, a* is greater than 0.80.

My own analysis of a data set similar to that used by LECLERC, using published figures and measurements of 52 species of *Chthonius* (*s.st.*) and *Kewochthonius* (*sensu* MUCHMORE), indicates an allometric relationship between *a* and absolute finger length [1]. A log-log plot of *a* against the length of the moveable finger (approximately the same length as the fixed finger) gives a good approximation to a straight line, with *a* decreasing as finger length increases (fig. 3). This is due to the positive allometric growth of the fixed finger proximad of *ist* relative to the region distad of this trichobothrium (the negative slope of the plot is an artefact caused by the use of the ratio instead of the absolute distance between *ist* and the fingertip).

Ontogenetic allometry of the chelal fingers has been demonstrated by several authors, notably VACHON (1943), MORIKAWA (1962), GABBUTT (1969, 1972) and MAHNERT (1981), in a variety of speudoscorpion species. In all of these studies it was found that most of the growth

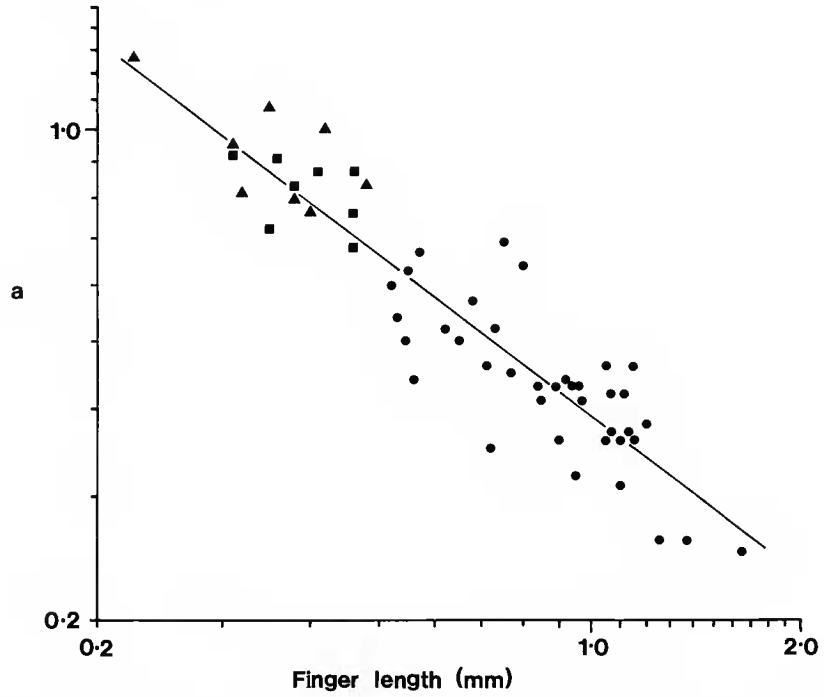


FIG. 3. — Plot of ratio *a* against length of moveable finger (log scales) in adults of *Chthonius* (*s. st.*) (species of *subterraneus* group excluded) and '*Kewochthonius*': circles, *Chthonius* species; squares, intermediate species; triangles, '*Kewochthonius*' species. Equation of regression line, $y = 0.39x^{0.17}$. See text for explanation.

1. Species of the *subterraneus* group have been excluded due to the strong curvature of their chelal fingers which makes comparable measurements difficult.

occured in the proximal region of the fingers. GABBUTT (1969, 1972) used the differential ontogenetic growth of the fingers of a number of neobisiids and chernetids to account for interspecific and intergeneric differences in the trichobothrial positions of the adults. MORIKAWA (1962) showed that the was little growth distad of *est* during the development of *Allochthonius opticus* (Ellingsen), the only chthoniid in which the growth of the fingers has been studied.

LECLERC (1983) seems to have be aware of the relationship between size and the relative position of *ist*. Noting that the adult of '*Neochthonius*' *chamberlini* is barely larger than the deutonymph, he stated : " On se trouve donc en présence d'une espèce ayant atteint sa taille d'adulte dès le stade deutonymphal ou dont la croissance est bloquée à ce stade (neoteny ?) " and that : " Cela pourrait expliquer, d'une part la petite taille des espèces de [*Neochthonius* and *Kewochthonius*] et, d'autre part, la position proximale des trichobothries *it* et *est* car on peut remarquer que le rapport *a* est " Neochthonien " pour les deutonymphes du genre *Chthonius* ; ce n'est qu'aux stades ultérieurs que sa valeur décroît ".

Unfortunately our knowledge of the relationships and ontogeny of the chthoniini are too meagre to permit such analyses of the polarity of size to be carried out. I have assumed that an increase in finger length has occured merely because this is more parsimonius than invoking neoteny.

The dentition of the fingers may also be size dependant, at least in part. Smaller ('*Kewochthonius*') species have closely spaced teeth, whereas larger ('*Chthonius*') species generally have more widely spaced teeth. Species intermediate between *Kewochthonius* and *Chthonius* in their *a* values usually have an intermediate form of dentition (e.g. *C. hungaricus* Beier, *C. pygmaeus* Beier, *C. ressli* Beier, *C. strinatii* Mahnert, *C. submontanus* Beier, and *C. thessalus* Mahnert). This would be expected if finger length increases without a 'compensatory' increase in the number (or size) of teeth. There are, however, some exceptions to this trend : a few species with long fingers also have a large number of closely spaced teeth (e.g. *Chthonius* (*C.*) *italicus* Beier).

Neither the dentition of the fingers nor the ratio *a* can be reliably used to distinguish *Kewochthonius* from *Chthonius* and both characters appear to be size related. *Kewochthonius* Chamberlin is reduced here to a junior subjective synonym of *Chthonius* (*s.st.*) (n. syn.).

The following species are here transferred to *Chthonius* (*Chthonius*) :

Chthonius halberti Kew, 1916 (see below).
C. (*Neochthonius*) *alpicola* Beier, 1931.
C. (*N.*) *caprai* Gardini, 1977.
C. (*N.*) *graecus* Beier, 1963.
C. (*N.*) *ilvensis* Beier, 1963.
C. (*N.*) *jonicus* Beier, 1931 (*C.* (*Kewochthonius*) *jonicus*, Mahnert, 1974; *C.* (*N.*) *jonicus*, Mahnert, 1979, 1982).
C. (*N.*) *karamanius* Hadzi, 1937.
C. (*N.*) *shulovi* Beier, 1963.
C. (*N.*) *tauricus* Beier, 1963.
Neochthonius chamberlini Leclerc, 1983, n. comb.
N. leoi Callaini, 1988, n. comb.

N. mauritanicus Callaini, 1988, n. comb.
N. paludis Chamberlin, 1929 (*C.* (*N.*) *paludis*, Beier, 1932; *Kewochthonius paludis* (syn. *C.* (*C.*) *pearsi* Hoff), Hoff, 1951), n. comb.

Two other species previously placed in *Chthonius* (*Neochthonius*) — *Chthonius* (*Mundochthonius*) *shelkovnikovi* Redikorzev, 1930 (Beier, 1932) and *C.* (*N.*) *pygmaeus* Beier, 1934 — have been transferred to *Chthonius* (s.st.) by Schawaller (1983) and Mahnert (1979) respectively.

This leaves a single species, *Kewochthonius spingolus* Schuster, 1962, from California, of uncertain taxonomic affinities. Judging from Schuster's description and figures, it probably belongs to *Chthonius* (*Hesperochthonius*) Muchmore, but a reexamination of the types will be necessary for the correct placement of this species.

Chthonius (Chthonius) halberti Kew, comb. rev.
(Fig. 11)

Chthonius halberti Kew, 1916 : 76-77, fig. 3.
Kewochthonius halberti; Chamberlin, 1929 : 65-66; Muchmore, 1968 : 71-75, figs. 1-3; Legg and Jones, 1988 : 56-58, figs 9A, 9B a-e.
Kewochthonius cf. *halberti*; Leclerc, 1983 : 49-50.
Chthonius (*Neochthonius*) *halberti*; Beier, 1932 : 46; 1963: 20-21, fig. 13.

Material examined : 1 ♂ "France, Banyuls-sur-Mer, Plage du Troque, L. Fage leg., M. Vachon det." (mounted on two slides MNHN Paris).

Description of male

Carapace as long as broad; epistome well developed, dentate, but not "fast halbkreisformig" (Beier, 1963 : 20); one pair of small anterior eyes visible; setae 4 : 6 : 4 : 2 : 6 (22), setae in posterior row of equal length.

Tergal setae 4 : 4 : 6 : 6 : 8 : 8 : 8 : 8 : 6 : 4 : 6 : 0.

Sternal setae 9 : mm22mm (5-6 along sides of notch) : mm6mm : 10 : 10 : 9 : 10 : 10 : 7 : 8 : 2.

Coxal setae P 2 (on manducatory process) + 3; I mmm + 3; II 4 (10-12 spines); III 6 (4 spines); IV 7; intercoxal tubercle bisetose.

Chelicera — fixed finger with 2 large, apical teeth and 5 small basal teeth; moveable finger with 1 isolated, distal tooth plus 1 large and 3 small basal teeth; spinneret a distinct tubercle; hand with 5 setae; *gs* present on moveable finger; flagellum with 10 blades.

Palp — chela as figured by Beier (1963 : fig. 13) except that the teeth do not form a lamella on either finger; fixed finger with about 63, moveable finger with about 53, contiguous, rounded teeth, decreasing in size proximally.

Leg IV setae 3 : 8 : 10 : 9; basitarsus TS 0.35, telotarsus TS 0.33.

Measurements (in mm) (ratios in parentheses) : body 1.1; carapace 0.36 × 0.34 (1.0); palp — femur 0.35 × ?, tibia 0.14 × ?, moveable finger 0.35; leg IV — basifemur 0.14 × 0.12 (1.2), telofemur 0.19 × 0.11 (1.7), tibia 0.18 × 0.05 (3.4), basitarsus 0.09 × 0.04 (2.2), telotarsus 0.15 × 0.03 (5.5).

This is almost certainly the specimen examined by BEIER (1963) for his redescription of *C. halberti*. Unfortunately, the palps have subsequently been crushed. MUCHMORE (1968) noted that the types of *C. halberti* differed from BEIER's (1963) description in the form of the chelal teeth and the epistome. These differences are due to errors in BEIER's description; the French specimen agrees well with MUCHMORE's description. The only apparent differences are in the TS ratios of the tarsi of leg IV which are slightly higher than the values given for the males from Ireland (basitarsus 0.38-0.42, telotarsus 0.40-0.42), though they fall within the range given for the females from England.

The apparently disjunct distribution of *Chthonius halberti* is probably due to its having been overlooked elsewhere; LEGG and JONES (1988) note that efforts to find it at the two known British localities have been unsuccessful. MAHNERT (pers. comm.) has collected it from a second French locality, 'Côte d'Azur, Beauvallon-sur-Mer, algae at sea-shore, 23 August 1979'.

Chthonius (Chthonius) ressli Beier

(Fig. 4-9)

Chthonius (*C.*) *ressli* Beier, 1956 : 24-25, fig. 1 (p. 32); 1963 : 32.
Chthonius (*C.*) *parvulus* Inzaghi, 1981 : 67-72, figs. 1-11; n. syn.

MATERIAL EXAMINED : holotype ♂ of *C. ressli* 'Niederosterreich, Purgstall, 20.10.1954, F. RESSL leg.' (Naturhistorisches Museum Wien); 1 ♂, 1 ♀, France, Charente-Maritime, La Rochelle, Parc Moulin des Pères (?), under stones beneath trees, August 1980, M. JUDSON leg. (MNHN, Paris).

DESCRIPTION OF FRENCH MATERIAL (♀ in parentheses)

Carapace about as long as broad; epistome large, dentate, denticulation extending along anterior margin; eyes difficult to see, but apparently with a weak pair of anterior eyes; setae 4 : 6 : 4 : 2 : 4 (20), lateral setae of posterior row shorter than the median setae.

Tergal chaetotaxy 4 : 4 : 4 : 4 : 6 : 6 : 6 : 6 : 1T2T1 : 4 : 1T2T1 : 0.

Sternal chaetotaxy 9 : ♂ mm23mm (6 setae along either side of notch) (♀ mm7mm) : mm7mm : m6m : m4m : m4m : s4s : 6 : 2T1T2 : 1T2T1 : 0.

Genitalia — ♂ typical, *ejca* relatively large; ♀ with lateral apodeme frame complete.

Coxal setae P 2 + 3; I mmm + 3; II 4 (7-8 spines); III 4 (2-3 spines); IV 7; intercoxal tubercle bisetose.

Chelicera — fixed finger with 9-11 teeth; moveable finger with 1 isolated, distal tooth and 9-10 basal teeth; galea a low tubercle; hand with 6 setae; serrula exterior composed of 13 blades.

Palp — setae of femur 5 : 2 : 5-6 : 3 : 1; setae of hand 4 posterior, 7 median and 4 anterior; fixed finger with 43 (40) teeth, moveable finger with 38 (36) teeth; sensorium of moveable finger opposite 11th (16th) tooth from base; a = 0.92 (0.91).

Leg I setae femur 9-10 (10); tibia 8; basitarsus 12.

Leg IV setae (basifemur to basitarsus) 3 : 7 : 10 : 9; basitarsus TS 0.36 (0.35); telotarsus TS 0.30 (0.28).

Measurements (in mm) (ratios in parentheses) : MALE : body length 0.85 ; carapace 0.29 × 0.27 ; palp — femur 0.31 × 0.06 (4.9), tibia 0.14 × 0.08 (1.8), hand 0.16 × 0.10 (1.7), chela length 0.47 (4.9), moveable finger length 0.31 (2.0 × hand) ; leg I — femur 0.17 × 0.04 (4.1), tibia 0.09 × 0.04 (2.4), basitarsus 0.10 × 0.03 (3.3), telotarsus 0.20 × 0.03 (7.8) ; leg IV — femur (total) 0.27 × 0.11 (2.3), tibia 0.18 × 0.05 (3.5), basitarsus 0.09 × 0.04 (2.3), telotarsus 0.19 × 0.03 (7.4). — FEMALE : body length 1.0 ; carapace 0.29 × 0.30 ; palp — femur 0.35 × 0.08 (4.3), tibia 0.16 × 0.09 (1.8), hand 0.19 × 0.12 (1.6), chela length 0.53 (4.5), moveable finger length 0.36 (1.9 × hand) ; leg I — femur 0.19 × 0.05 (4.2), tibia 0.09 × 0.04 (2.1), basitarsus 0.10 × 0.03 (3.1), telotarsus 0.22 × 0.03 (8.6) ; leg IV — femur (total) 0.29 × 0.13 (2.3), tibia 0.20 × 0.06 (3.6), basitarsus 0.10 × 0.04 (2.4), telotarsus 0.20 × 0.03 (7.5).

Examination of the holotype of *C. ressli* reveals two errors in BEIER's original description (1956, repeated 1963). Although the specimen is in poor condition (right chela and tibia lost, body covered in small crystals), it is clear that the teeth of the chela do not form a lamella and that the chaetotaxy of the tergites is normal (tergite IV with 4 setae, not 6 as stated by BEIER). The following details can be added to BEIER's description : palp — femur 0.33 × 0.08 (4.2), hand 0.17 × 0.10 (1.7), moveable finger 0.35 (2.0 × hand), chela 0.51 (5.0) ; dentition as described above for French specimens ; leg IV — basitarsus TS 0.36, telotarsus TS 0.28.

With these corrections it becomes apparent that *Chthonius parvulus* Inzaghi (types from Italy, Bergamo ; subsequently collected at Emilia, Besenzone, PC, 17 June 1979, S. INZAGHI leg.) is a junior subjective synonym of *C. ressli* Beier. The only difference between INZAGHI's (1981) description and the specimens examined here lies in the development of the eyes. INZAGHI described the eyes of *C. parvulus* as "anterior con lenti... posteriori ridotti a machie oculari" which contrasts with the poorly developed (possibly absent) eyes of *C. ressli* specimens from Austria and France. This may simply be due to the state of preservation of the different collections. Given the close agreement between all other characters, it seems reasonable to conclude that the two species are synonymous.

Chthonius ressli is very similar to *Chthonius* (*C.*) *strinatii* Mahnert, 1975, from a cave in Greece. The female of *C. strinatii* can be distinguished from that of *C. ressli* by the absence of contiguous teeth at the tip of the fixed finger, the lower number of chelal teeth (fixed finger with 32, moveable finger with 30 in *strinatii*) and by the relatively shorter fingers of the chela (1.52 − 1.54 × hand in *strinatii*).

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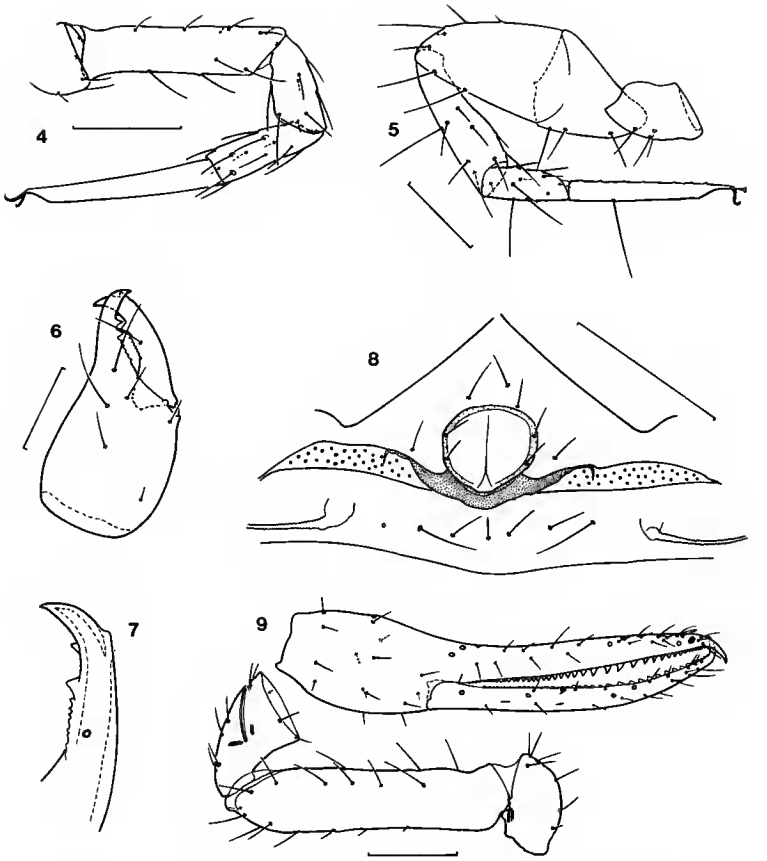
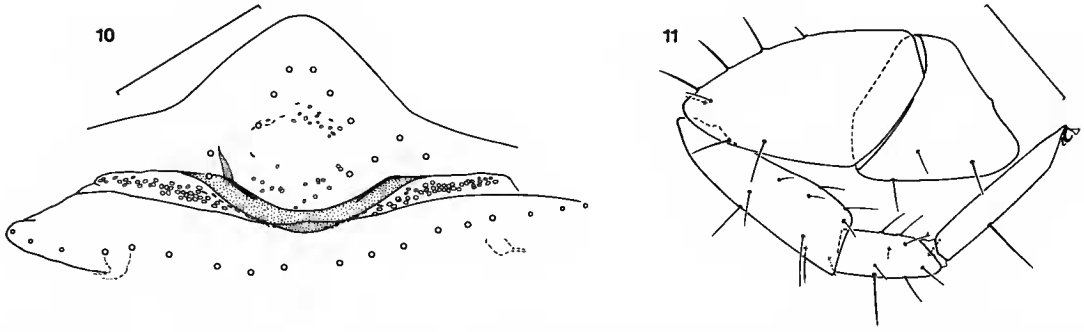


FIGS. 4-9. — *Chthonius ressli* Beier, female (La Rochelle) : 4, right leg I; 5, right leg IV; 6, right chelicera; 7, moveable finger of chelicera (male); 8, genitalia; 9, left palp. (Scale lines equal 0.1 mm.)



FIGS. 10-11. — 10, *Neochthonius stanfordianus* Chamberlin, female genitalia; 11, *Chthonius halberti* Kew (Banyul-sur-Mer), right leg IV, male. (Scale lines equal 0.1 mm.)

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